BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 4 NOVEMBER 2011 NUMBER 527

A NEW DWARF *AGAMA* (SAURIA: AGAMIDAE) FROM ETHIOPIA

PHILIPP WAGNER[1,2] AND AARON BAUER[1,3]

ABSTRACT. A new dwarf lizard of the genus *Agama* Daudin, 1802 (Sauria: Agamidae), is described from central Ethiopia. This dwarf agama (< 59 mm snout–vent length [SVL]) was compared with other dwarf congeners (< 65 mm SVL) in West, Central, and East Africa and to medium-sized agamas (< 92 mm SVL) occurring in the Horn of Africa. The new species is characterized by a homogeneous body scalation; keeled but nonmucronate dorsal scales; smooth ventral, gular, and upper head scales; and having the nasal scale on the canthus rostralis. It is morphologically well differentiated from all congeners to which it was compared in having a nuchal crest, few tufts of short spinose scales, and the nasal scale on the canthus rostralis and can further be identified by its large occipital scale, smooth gular and ventral scales, and keeled, but not strongly mucronate or spinose, dorsal scales. The new species may live in colonies, like many of the larger rock *Agama* species, and based on the presence of multiple age classes at the same time of year, it is probably not an annual species, as are some other dwarf *Agama*. The affinities of the new species are unclear but, on zoogeographic grounds, may lie with congeners to the west of the Rift Valley.

KEY WORDS: Agamidae; *Agama*; *A. bottegi*; *A. hartmanni*; *A. persimilis*; *A. rueppelli*; *A. gracilimembris*; *A. weidholzi*; *Agama* sp. nov.; Africa; Ethiopia; new species

The Horn of Africa is a peninsula in East Africa jutting into the Arabian Sea and lying along the southern side of the Gulf of Aden. It is the easternmost projection of the African continent and encompasses the countries of Eritrea, Djibouti, Ethiopia, and Somalia. Its lowlands are dominated by arid and semi-arid habitats in spite of their proximity to the Equator. Monsoon winds lose their moisture before reaching Djibouti and Somalia, with the result that most of the Horn receives little rainfall during the southeast monsoon season (June to end of August).

The Horn is the greatest hotspot of African agamids and certain other lizards

[1] Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, U.S.A.; e-mail: aaron.bauer@villanova.edu

[2] Zoologisches Forschungsmuseum A. Koenig, Adenauerallee 160, D-53113 Bonn, Germany; e-mail: philipp.wagner.zfmk@uni-bonn.de

[3] Research Associate, Department of Herpetology, Museum of Comparative Zoology, 26 Oxford Street, Cambridge, Massachusetts 02198, U.S.A.

© The President and Fellows of Harvard College 2011.

SHOUT
SHARE
IT

(Lanza, 1983), e.g., the gekkonid genus *Hemidactylus* (Bauer et al., 2010). Apart from *Laudakia* Gray, 1845, all African agamid genera are present in the area (see Wagner, 2010), including the regionally endemic *Xenagama* Boulenger, 1885. The highest species diversity occurs in *Agama* Daudin, 1802 (seven species), and *Acanthocercus* Fitzinger, 1843 (six species), whereas *Trapelus* Cuvier, 1816, and *Pseudotrapelus* Fitzinger, 1843, are each represented by only a single species (Largen and Spawls, 2010; Wagner, 2010). All agamid lizards inhabiting the Horn are adaptated to arid habitats, and most of them occur in rocky savannahs. *Uromastyx* Merrem, 1820, inhabits deserts and *Xenagama* dry woodland to semidesert, whereas *Acanthocercus atricollis minutus* (Klausewitz, 1957) and *A. atricollis loveridgei* (Klausewitz, 1957) are most likely tree dwellers. For most species, our knowledge of ecology is too meager to discuss ecological adaptations, but a high degree of variation in morphology is obvious. The size of the agamid lizards in the Horn ranges from the small *Agama persimilis* Parker, 1942 (snout–vent length [SVL] max. 64 mm), to medium-sized lizards (e.g., *Xenagama*; SVL max. 90 mm), to the large *Uromastyx* (SVL max. 174 mm), the latter both characterized by thick, armored tails, but most of the other species are very conservative in body shape and similar to the widespread genus *Agama* Daudin, 1802.

Because of the limited information available about agamid lizards in Africa and especially those occurring in the Horn, museum vouchers from the area are of special interest. The Museum of Comparative Zoology (MCZ) holds a series of specimens initially identified as "*Agama agama agama*" from Ethiopia. According to Largen and Spawls (2006, 2010) *Agama agama* (Linnaeus, 1758) is present in Ethiopia, but this is, in fact, an artifact of the use of an older taxonomic concept of this species (see Wagner, 2011). Wagner et al. (2011) have shown that *Agama finchi* Böhme et al., 2005, is the only representative of the *A. agama* s. str. species group in the Horn. The MCZ series consists of quite small specimens (SVL 25.0–58.6) that might be mistaken for juveniles, but it includes one obviously gravid female. Therefore, this series is distinctly smaller than most other *Agama* species known from the Horn and comparable in size only to dwarf species of the genus.

Only a few dwarf species of *Agama* are known. *Agama weidholzi* Wettstein, 1932 (SVL max. 65 mm), is only known from a restricted area in Senegal, Gambia, western Mali, and Guinea-Bissau (for a detailed distribution, see Wagner et al., 2009). It is easy to identify by its large white-bordered dark patch on the shoulders and the thin vertebral stripe in males. Another dwarf *Agama* is *A. gracilimembris* Chabanaud, 1918 (SVL max. 57 mm), described from Benin and now known from further east in Nigeria (Grandison, 1969; Gartshore, 1985), Cameroon (Böhme, 1975), and the Central African Republic (Joger, 1990; see also species account herein). Both species are among the rarest members of the genus in Africa, and information about their habitat preferences, behavior, and distribution is limited. Relationships between the two dwarf species have not yet been investigated. Grandison (1969) assumed a close relationship based on morphology, but Wagner et al. (2009) have shown that *A. weidholzi* is closely related to the Guinean *Agama cristata* Mocquard, 1905, and *Agama insularis* Chabanaud, 1918 (however, *A. gracilimembris* was lacking from their analysis).

Three other dwarf to medium-sized *Agama* occur in the Horn of Africa: *A. persimilis* (SVL max. 64 mm), *Agama hartmanni* Peters, 1869 (SVL max. 92 mm), and *Agama rueppelli* Vaillant, 1882 (SVL max. 88 mm).

Their relationships are also unknown but are under investigation by the authors. All three are solitary, only establishing territories during the breeding season (Wagner, unpublished data) and are, therefore, distinct in behavior relative to the mostly larger (SVL 80–145 mm) rock *Agamas*. All are poorly known, but it is uncertain if they are truly rare or only underrepresented in museum collections. *Agama rueppelli* is the most common, but *A. persimilis* and *A. hartmanni* are only known from a small number of vouchers from a handful of localities. Two other species occurring in the Horn, *Agama cornii* Scortecci 1928 and *Agama bottegi* Boulenger, 1897, are only known from a few specimens each, and their taxonomic status is questionable. Because all these lizards are poorly known, a short review of each species including information from museum vouchers and literature is presented herein to facilitate the comparison of these taxa with the MCZ series of "*Agama agama agama*" from Ethiopia and to help establish the identity of the members of this series.

MATERIAL AND METHODS

Material. Specimens from the following institutes were examined or referenced for locality data (see Appendices 1 and 2): California Academy of Sciences (CAS), San Francisco, California, U.S.A.; Museo Civico di Storia Naturale di Genova, Italy (MSNG); Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, U.S.A.; Muséum d'Histoire Naturelle (MHNG), Genève, Switzerland; Muséum Nationale d'Histoire Naturelle (MNHN), Paris, France; Naturhistorisches Museum Wien (NHMW), Vienna, Austria; Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn, Germany.

Name-bearing types of the following taxa were examined for comparison: *A. bottegi*, *A. cornii*, *A. gracilimembris*, *A. hartmanni*, *A. persimilis*, *A. rueppelli rueppelli*, *Agama rueppelli septentrionalis* and *A. weidholzi* (see Appendix 1).

Moreover, data and descriptions presented by Parker (1942), Grandison (1968, 1969), Lanza (1978), Gartshore (1985), and Largen and Spawls (2010) and relevant original descriptions (Peters, 1869; Vaillant, 1882; Boulenger, 1897; Chabanaud, 1918; Scortecci, 1929; Wettstein, 1932; Parker, 1942) were consulted. Distributional data were based on specimens examined (Appendix 1), reliably determined but unexamined specimens in museum collections (Appendix 2), and additional literature sources (Appendix 3).

Digital X-ray images of specimens were obtained using a Faxitron closed cabinet X-ray (LX-60, Faxitron Corp.) with a Varian flat-panel digital X-ray detector.

Measurements. Scale counts and terminology follow Grandison (1968), and measurements were taken with callipers to the nearest 0.1 mm. The following values were used: SVL, from tip of snout to cloaca; head width (HW), measured at the point of greatest width; head height (HH), measured at the point of greatest height; head length (HL), measured from behind the tip of retroarticular process to tip of snout; tail length (TL), measured from posterior lip of cloaca to tip of tail; supralabials (SL), number of all supralabial scales; infralabials (IL), number of all sublabial scales; scales around midbody (SaM), number of scale rows around body midway between the limbs; precloacal pores (PP), number of rows and number of pores in total; subdigital lamellae (SDL), number of lamellae under the fourth toe or finger, respectively; ventral scales (VS), longitudinal ventral scales along midbody from shoulders to cloaca; dorsal scales (DS), longitudinal dorsal scales along midbody from shoulders to cloaca.

RESULTS

The specimens of the unknown dwarf *Agama* from Ethiopia were compared in detail with the other dwarf congeners (*A. gracilimembris, A. persimilis, A. rueppelli, A. weidholzi*, see also table 1) as well as with the medium-sized *A. hartmanni*, with which it shares similarities of head and body scalation. Two other rarely mentioned taxa, *A. cornii* and *A. bottegi*, were also included in the comparison. As noted by other authors (e.g., Largen and Spawls, 2010, see also species account below), *A. cornii* has been recognized as a synonym of *A. hartmanni* because the type and sole specimen of the former species is identical with respect to relevant characters with the types of the latter. The status of *A. bottegi* is still doubtful. The name-bearing type was examined, and additionally the original description and illustration shows that *A. bottegi* is clearly distinct from the other taxa compared herein (e.g., large nuchal and dorsal crests present; see species account below). A comparison of the head scalation between dwarf species mentioned above revealed differences in scale tufts, nuchal crest, and head scales (see Fig. 1) with respect to MCZ R-146685–89 (see species accounts). Other regional congeners could be excluded on the basis of size and other features, and we thus recognize this Ethiopian dwarf *Agama* as a new species, which we describe below.

SYSTEMATICS

Agama persimilis Parker, 1942

Holotype. BMNH 1937.12.5.64, adult female, from "45°50′E × 8°N in the Haud [north-eastern part of Ogaden, Somali region Ethiopia]," collected by Capt. R.H.R Taylor on 25 XI 1934.

Diagnosis (partly fide Parker, 1942). A dwarf *Agama* reaching a total length of about 160 mm, females (SVL 56–64) are larger than males (SVL 43–54). Body strongly depressed, hind limbs long. Gular pouch absent. Tail about 65% of the total length, very broad at its base, tapering sharply. Head convex with the upper surface of the snout flat. Head scales on the upper parts moderately large, with the occipital scale enlarged. Nostril, directed upward and backward, pierced in the posterior part of a nasal scale above the canthus rostralis. Usually with one scale between the nasal and the first supraciliary scale. Scales of the supraocular region longitudinally elongate, with a dull keel. Nuchal and dorsal crests absent. Ear as large as the eye opening, superficial and completely exposed. Lower and posterior borders of the ear as well as the sides of the neck with tufts of spines, longest spines about half the length of the eye opening. Tufts of spines not encroaching upon the ear opening. Body scales large, homogeneous, imbricate, keeled, and mucronate, with 52–57 scale rows around midbody. Thirty vertebral scales between the insertions of the limbs. Gular and ventral scales smooth, ventrals much smaller than the dorsals. Lamellae 16–18 under fourth toe, third and fourth toes nearly equal in length. Males with one row of 10–12 precloacal pores.

Distribution. Eastern Ethiopia, Somalia, and E/NE Kenya (see Fig. 2).

Agama hartmanni Peters, 1869

Syntypes. ZMB 4355 (three specimens, holotype not designated), from "Dongola [Sudan]," collected by Dr. Hartmann and [Adalbert] von Bamim.

Synonym. Agama cornii Scortecci, 1929, Holotype: MCM 1193, from "Um Ager, [Om Ager, Eritrea]," collected by the "Missione Corni, Calciati."

Diagnosis (partly fide Peters, 1869). A poorly known, medium-sized agamid lizard reaching a total length of 230 mm and a SVL up to 92 mm, with a depressed body and

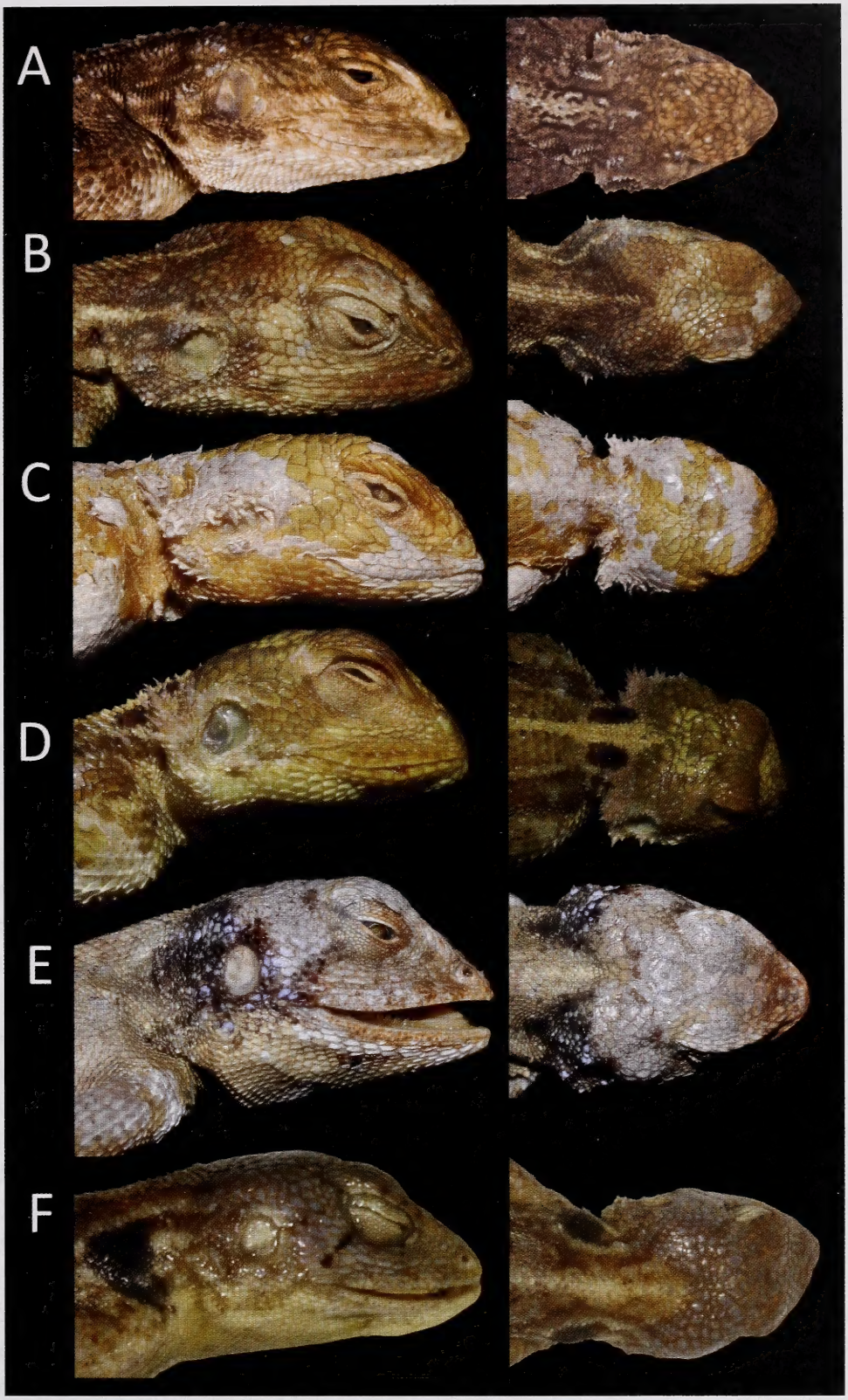

Figure 1. Comparison of head scalation in dwarf and selected medium-sized agamas discussed in this paper (images are not the same scale): A, *Agama* sp. nov. (MCZ R-146689); B, *Agama hartmanni* (BMNH 1913.9.16.9); C, *Agama rueppelli* (BMNH 1946.8.24.50, syntype); D, *Agama persimilis* (BMNH 1937.12.5.64, holotype); E, *Agama gracilimembris* (MNHN 1904.0115, syntype); F, *Agama weidholzi* (MCZ R-44311, paralectotype).

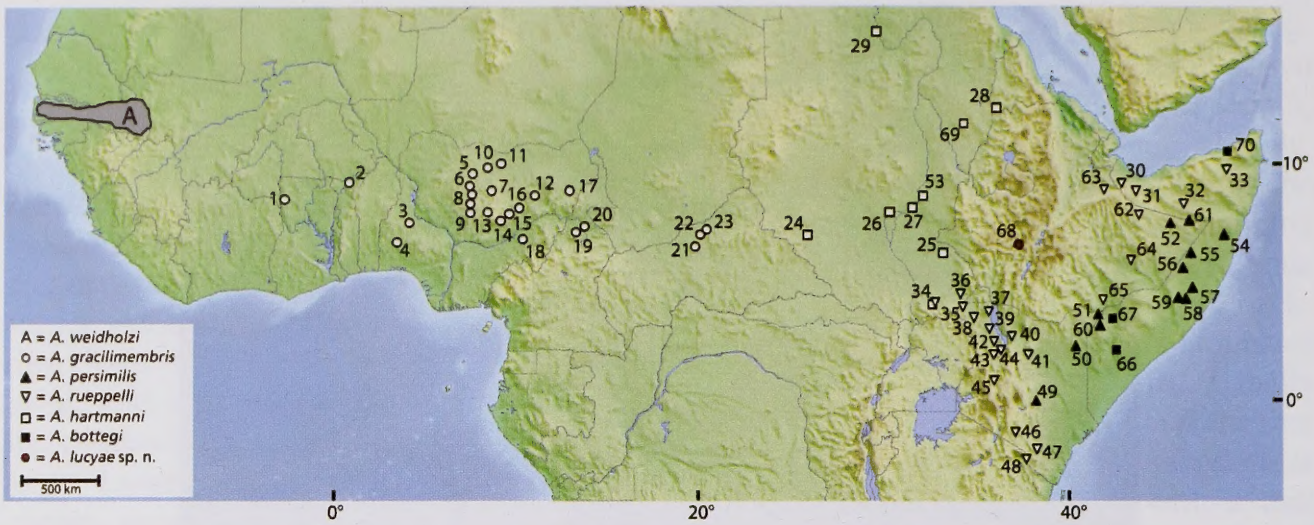

Figure 2. Distribution of relevant dwarf or medium-sized *Agama* lizards. A, the entire distribution area of *A. weidholzi*; for locality details, see Wagner et al. (2009). 1, Wa; 2, Pendjari NP; 3, Igbetti; 4, Ado-Awaiye; 5, Kura; 6, Samaru; 7, Falgore; 8, Zaria; 9, Anara; 10, Kano; 11, Ringim; 12, Yankari; 13, Zonkwa; 14, Lafia; 15, Pandam; 16, Shendam; 17, Hung; 18, Wukari; 19, Boki; 20, Benue NP; 21, between Kotissako and Sakoumba; 22, Ndelé; 23, Koumbala; 24, Bahr el Ghazal; 25, Boma Hills; 26, Bahr el Zeraf; 27, Taufikia; 28, Omhajer; 29, Dongola type locality; 30, Boorama; 31, Hargeysa Airport; 32, Buq Village; 33, Buran District; 34, Bahr-el-Gebel; 35, Lokichoggio; 36, Lokomarinyang; 37, Lokitaung; 38, Lokori; 39, Lodwar; 40, Loyengalani; 41, Marsabit; 42, Loperot Kalabata; 43, Kakuma; 44, Kanapoi; 45, Lake Baringo; 46, Kajiado; 47, Voi; 48, Mbunyi; 49, Ngomeni; 50, Wajir; 51, Mandera; 52, Haud, type locality; 53, Kodok; 54, Geribàn; 55, Har Addèi; 56, 55 km N-NE of Dùsa Marèb; 57, El Bur [Ceel Buur]; 58, Bud Bud; 59, Iesòmma; 60, Harò; 61, Bohodle; 62, Sassabana; 63, Gumboworen; 64, Dabanac; 65, confluence of the Web and the Ganana [Ganale]; 66, Dinsór; 67, Lugh [Luug], type locality; 68, 58 km NW of Soddo, type locality; 69, Singa; 70, Karin.

moderately long limbs. Gular pouch absent. Head convex, not as flat as in *A. rueppelli* or *A. persimilis*. Tail about 60% of total length. Head scales moderately large, smooth, with the occipital scale usually enlarged. Nostril nearly as large as the nasal scale, round, directed dorsally and laterally, pierced in the middle of the nasal scale, situated on the canthus rostralis. Usually one to two scales between nasal and first supraciliary scales, supraciliary scales smooth. Nuchal and dorsal crest absent. Ear opening smaller than the eye, superficial and completely exposed. No tufts of spinose scales near the ear or on the neck, a few single erect scales scattered near the ear opening. Body scales homogeneous, keeled, mucronate, and erect, with 76–81 scale rows around midbody, ventral smaller than dorsal scales. Gular and ventral scales smooth. Males with 9–12 precloacal pores. Third and fourth toes nearly equal in length, 16–21 lamellae under fourth toe.

Distribution. Sudan, South Sudan, Eritrea (see Fig. 2 for details).

Remarks. Wermuth (1967) considered *A. cornii* a doubtful species and the status remained dubious until Moody (1980) synonymized it with *A. hartmanni* without explicit justification. Because Moody's (1980) doctoral dissertation was never published, this taxonomic act has been largely overlooked. Barts and Wilms (1997) mentioned it again as a valid species and later Largen and Spawls (2010:239) mentioned *A. cornii* as an invalid name and treated it as a synonym of *A. hartmanni*. We reexamined the holotype of *A. cornii* and compared it with the description and types of *A. hartmanni* (Peters, 1869). Based on this examination we follow Moody (1980) and Largen

and Spawls (2010) in recognizing *A. cornii* as synonym of *A. hartmanni*. No differences were found between the single type specimen and specimens of the latter nominal species, and both share all characters mentioned above.

Agama rueppelli Vaillant, 1882

Syntypes. MNHN 5897; BMNH 1946.8.24.50 (syntypes, see remarks below), from "Bender-Meraya, Pays Comalis [=Somalia]."

Synonym. Agama vaillanti Boulenger, 1895. Lectotype: MSNG 28850, adult male, from "Ogaden," Ethiopia.

Diagnosis. A medium-sized *Agama* with a maximum total length of 280 mm. Males (58–88 mm SVL) smaller than females (76–88 mm SVL). Body depressed, hind limbs long. Tail more than 65% of total length, very broad at its base, tapering sharply. Gular pouch absent. Head convex, with the upper surface of the snout flat. Head scales smooth, equal to ventral scales, with the occipital scales variable in size (equal to other head scales to slightly enlarged). Nostril directed posterodorsally, completely visible from above, pierced in the posterior part of a large nasal scale, situated above the canthus rostralis. Usually with one to two scales between nasal and first supraciliary scales. Supraciliary scales smooth. Nuchal and dorsal crest absent. Ear opening only half the size of the eye, surrounded by tufts of spinose scales hiding the tympanum. Body scales large, homogeneous, keeled, mucronate, and erect, in 54–64 scale rows around midbody. Vertebral scales 59–66. Gular and ventral scales smooth, ventrals smaller than dorsal scales. Lamellae 14–16 under the fourth toe, third and fifth toes nearly equal in length. Males with one row of 9–13 precloacal pores.

Distribution. Sudan, South Sudan, Ethiopia, Somalia, and Kenya (see Fig. 2).

Remarks. Three different subspecies are currently recognized (Largen and Spawls, 2010), but their status is questionable. Therefore, we only refer to *A. rueppelli*, but a review of the species is needed.

Guibé (1954), in his agamid type catalogue of the Paris museum, incorrectly regarded the single MNHN syntype as the holotype. Later, Brygoo (1988) indicated that the second syntype of *A. rueppelli* left the Paris collection in 1895 without a documented destination, and Brygoo (1988) was unaware of its present whereabouts. Boulenger (1895) in his description of *A. vaillanti* mentioned that he was "able to compare the specimen with one of the types of *A. rueppelli*," and obviously this type is the one donated or exchanged from the Paris collection.

Agama bottegi Boulenger, 1898 [1897] incertae sedis

Holotype. MSNG 28548, adult male, from "Lugh" (03°47′46N, 42°32′32E), Somalia, collected by Capt. U. Ferrandi (V. Bòttego Expedition).

Diagnosis (fide Boulenger 1898 [1897]). A large *Agama* with a maximum length up to 355 mm (SVL 120 mm). Head moderately convex, body scarcely depressed, hind limbs strong. Gular pouch absent. Tail twice as long as SVL. Head convex, snout not flat as in *persimilis*. Head scales moderately large, smooth, with the occipital scale enlarged. Nostril tubular, directed backward; pierced in the posterior part of a small nasal scale, situated on the canthus rostralis. Two scales between the nasal and the first supraciliary scale. Supraciliary scales smooth. Strong nuchal crest present in males, with conical scales equal to the diameter of the ear opening. Low crest extending down the back and to the tail. Ear opening larger than the eye. Tufts of spinose scales near the ear and on the sides of the neck present, longest spines about two-third the diameter of the

ear opening. Body scales large, homogeneous, imbricate, strongly keeled, and strongly mucronate; in 53 rows around midbody. Ventral scales keeled, smaller than the dorsals. Fourth and third fingers equal, fourth toe slightly longer than third, fifth not extending beyond first. Tail slightly compressed, covered with strongly keeled scales, which are larger than the body scales. One row of precloacal pores.

Distribution. Only known from the type locality and two other localities (see Fig. 2).

Remarks. This species is clearly distinct from the MCZ series from the Omo River Valley in aspects of size, scalation characters (e.g., large crests, strongly mucronate scales and tufts with long spinose scales), and coloration, but it is similar in some aspects (e.g., strong nuchal crest, tufts of long spinose scales) to *Agama spinosa* Gray, 1831.

Agama gracilimembris Chabanaud, 1918

Syntypes. MNHN 04.114–115, male and female, from "Dahomey [=Benin]," collected by Eugéne Mégy in 1904.

Diagnosis (partly fide Grandison, 1968). A dwarf *Agama* with females (SVL 48–57 mm) longer than males (SVL 40–47 mm). Body depressed, hind limbs long. No gular pouch in males or females, but a marked lateral fold is present. Tail one and a half times longer than SVL. In males, base of the tail with prominent hemipeneal bulge. Head convex. Upper head scales large, strongly keeled. Occipital scale enlarged, greatest width as large as the diameter of the ear opening. Nostril directed posteriorly, pierced in the posterior part of the nasal scale which is below the canthus rostralis. Usually with one scale between the nasal and the first supraciliary scale. Supraciliary scales smooth. Nuchal and dorsal crests absent. Ear opening as large as the eye, tympanum superficial and exposed. Tufts of long, spinose scales around the ear and the sides of the neck lacking. Single, short, conical scales close to the border of the ear opening are present. Body scales small, heterogeneous, keeled, and nonmucronate, in 70–85 scale rows around midbody. Enlarged body scales irregularly intermixed on the lateral regions of the body. Vertebral scales 30–46. Gular and ventral scales strongly keeled, ventrals about the same size as the dorsal scales. Hind limbs relatively long, reaching the tympanum. Lamellae 13–14 under fourth toe. Males with one row of 8–12 precloacal pores.

Distribution. Ghana, Benin, Nigeria, Cameroon, Central African Republic (see Fig. 2 for details).

Agama weidholzi Wettstein, 1932

Lectotype. NHMW 18318, from "Urwald Sumpfgebiet, Tabadienké, 30 km S Diallakoto, Senegambien [=Senegal]," collected by Weidholz in 1930.

Diagnosis (partly fide Grandison, 1969). A dwarf *Agama* species with females (SVL 56–65 mm) longer than males (SVL 54–62 mm). Body depressed, hind limbs long, reaching the area between ear opening and eye. No gular pouch. Tail one and a half times longer than SVL. Head convex. Upper head scales large, keeled; occipital scale enlarged, as large as ear opening. Nostril directed dorsolaterally, pierced in the posterior part of a long, slightly oval, swollen nasal scale below the canthus rostralis. Usually with one scale between the nasal and the first supraciliary scale. Supraciliary scales smooth. Nuchal and dorsal crests absent. Ear opening as large as the eye, tympanum superficial and exposed. Tufts of spinose scales absent from sides of neck. Sometimes one or two conical scales behind the ear hole. Body scales small, homogeneous (but tendency for rows of enlarged vertebral scales), keeled and nonmucronate, in 68–82 rows around midbody. Vertebral scales 32–48, 16–21 lamellae under fourth toe, and males with 6–10 precloacal pores usually in one row.

Distribution. Senegal, The Gambia, Guinea-Bissau, and Mali (for details see Fig. 2; Wagner et al., 2009).

Agama lucyae, new species

Holotype. MCZ R-146689, young adult male. Ethiopia: "Wollega" [probably Shewa or Kefa province; see remarks in Distribution section] today either Oromiya or Southern Nation, Nationalities and Peoples' Region, Omo River, 58 km NW of Soddo [=Sodo], about 1,300 m above sea level (a.s.l.). Coordinates: 7.27085°N, 37.37891°E [subsequently georeferenced, see remarks in Distribution section]. Collected: 21.VII.1964, by T. Monath.

Paratypes. MCZ R-146687, adult female; MCZ R-146685, subadult female; MCZ R-146688, subadult male; MCZ R-146686, juvenile male. All with same collecting data as holotype.

Diagnosis. A small *Agama* lizard (body length of males up to 53.5 mm SVL, females to 58.5 mm SVL), with a short depressed head, smooth head scalation, a large occipital scale, homogeneous body scalation, and strongly keeled but non- or only slightly mucronate dorsal scales. The nasal scale is on the canthus rostralis. Ear hole surrounded by single short conical scales; few tufts of spinose scales behind the ear and on the lateral side of the neck are present, tympanum superficial. Short neck crest present in both sexes. Gular and ventral scales smooth. Tail not arranged in distinct whorls.

Differential Diagnosis. A. lucyae sp. nov. is distinct from *Acanthocercus*, *Xenagama*, and *Uromastyx* in lacking distinct whorls or regular rings on the tail and from *Acanthocercus* by its large occipital scale. It differs from *Pseudotrapelus* by its smaller size (58.5 versus 88 mm SVL), its relatively larger body scales, the tufts and single conical scales around the ear and on the side of the neck versus the absence of these scales, and the relatively shorter hind limbs (38.5 versus 77 mm). It is distinct from African *Trapelus* species by its large ear hole, the visible tympanum, and the tufts and single conical scales around the ear and on the side of the neck.

The new taxon is smaller than most other *Agama* species occurring in the Horn. It is distinct from *Agama robecchii* in its homogeneous body scalation and larger dorsal body scales; it differs from *Agama doriae*, *A. finchi*, *Agama lionotus*, *A. bottegi*, and *A. spinosa* by possessing a smaller number of tufts of shorter spinose scales behind the ear and on the sides of the neck, and nonmucronate body scales; it further differs from *A. spinosa* and *A. bottegi* by a much smaller nuchal crest and from the latter in not possessing a body and tail crest. It is very clearly distinct from all these species in color pattern, which is characterized by a vertebral stripe and, in males, longitudinal stripes and transverse bands.

Agama lucyae sp. nov. differs from other dwarf or medium-sized *Agama* lizards as follows: from the slightly longer *A. rueppelli* by its non- or only slightly mucronate dorsal body scales versus mucronate and spiny scales, by the development of scale tufts behind the ear opening and on the sides of the neck (few short tufts versus many long tufts), a higher number of scale rows around midbody (66–69 versus 54–64), a lower number of vertebral scales (47–52 versus 59–66), and the presence of a nuchal crest; from *A. persimilis* by having an acuminate snout (versus a rounded), nuchal crest present, higher numbers of scale rows around midbody (66–69 versus 52–57) and vertebral scales (47–52 versus 26–31), few tufts of shorter spinose scales (versus tufts of long scales around the ear), and a distinct coloration (neither the dark patches on either side of the vertebral stripe nor the large brown patch on the anterior flanks of *A.*

persimilis are obvious in *A. lucyae* sp. nov.); from *A. hartmanni* by its smaller size (53.5–58.5 versus 87–92 mm SVL), nuchal crest, tufts of spinose scales behind the ear opening and on the neck, and lower numbers of scale rows around midbody (66–69 versus 76–81) and vertebral scales (47–52 versus 61–68); from *A. weidholzi* by having the nasal scale on the canthus rostralis (versus below the canthus rostralis), the upper head scales smooth, tufts of spinose scales behind the ear opening and on the neck, a nuchal crest, a slightly overlapping range but higher mean number of vertebral scales (47–52 versus 32–48), a lower mean number but slightly overlapping range of scale rows around midbody (66–69 versus 68–82), and the remarkable lack of a white bordered black patch on the shoulders; and from *A. gracilimembris* by its homogeneous body scalation, nasal scale on the canthus rostralis (versus below the canthus rostralis), having the upper head, ventral and gular scales smooth, possessing tufts of spinose scales behind the ear opening and on the neck, neck crest present, and a lower number of scale rows around midbody (66–69 versus 70–85), but a higher number of vertebral scales (47–52 versus 30–46).

Description of the Holotype. MCZ R-146689 (see Fig. 3), young adult male, tail broken 19 mm from the base.

Measurements. SVL: 53.5 mm, HH: 7.5 mm, HW: 12.2 mm, HL: 16.6 mm, length of left forelimb: 25.5 mm, length of left hind limb: 38.5 mm.

Description. Head and body depressed. Nostril tubular, directed laterally and slightly posterodorsally, pierced in the posterior part of a large convex, smooth, pear-shaped nasal scale which is situated on the canthus rostralis. Nasal scale partly visible from above, directly in contact with the first canthal scale. The first two canthal scales not in contact with the eye. Scales on the head smooth, somewhat rugose, interorbital scales as large or larger than the supraorbital scales; imbrications of temporal scales not uniformly directed, partly ventrally, others posteriorly. Occipital large, its greatest width equal to the diameter of the tympanum, pierced by a visible pineal foramen in the center. 10 (left)–8 (right) upper and 9 (left)–8 (right) lower labial scales. Ear opening as large as the eye, surrounded at its border by several single short conical scales, one tuft above, and one tuft of short spinose scales behind the ear opening, three of these tufts on the dorsolateral parts of the neck. Spinose scales of the tufts short, often consisting of scales of the same size, sometimes one longer scale in the center. Gular fold present, but gular pouch absent. Short nuchal crest present, composed of nine short erect scales. Dorsal scales homogeneous, in 67 scale rows around midbody, in 52 dorsal scales along the vertebrate and 68 ventral scales along the belly between the anterior border of the shoulders and cloaca. One row of eight precloacal pores. Dorsal body scales keeled, with a keel extending along the entire scale, not or only uncommonly very slightly mucronate and erect. Gular scales smooth, ventral scales smooth, becoming feebly keeled toward the lateral side of the body. Hind limb and fourth toe long, reaching to the posterior part of the tympanum when adpressed. Lamellae 16 under the left fourth finger, 17 lamellae under the left fourth toe. Relative length of digits of left manus $4 > 3 > 5 > 2 > 1$; relative length of digits of left pes $4 > 3 = 5 > 2 > 1$; Tail depressed at its base, broken 19 mm behind cloaca. Large hemipeneal pockets absent. Dorsal tail scales strongly keeled, slightly mucronate, somewhat larger than the body scales, and not arranged in whorls.

Coloration (after formalin fixation and ethanol preservation). Upper parts of the body and head brownish, a pale vertebral

Figure 3. Holotype of *Agama lucyae* sp. nov. (MCZ R-146689). A, Dorsal view; B, ventral view; C, lateral view; D, ventral view of head and chest; E, dorsal view of head and chest; F, lateral view of head.

stripe from just behind the occiput along the body and extending on the tail is visible. At the neck, the pale vertebral stripe is bordered by a dark band on each side. A small dark patch under both ear openings is visible. A faintly juvenile coloration is present, with four dark transverse bands between the limbs. On these bands, several pale, darkly bordered ocelli are visible. Throat whitish, with a dark reticulated pattern that extends to the entire belly and partly to the underside of the hind limbs. The pattern is somewhat darker at the base of the throat, forming a dark patch.

Variation of Paratypes. Adult female. Gravid, containing a minimum of five eggs (see X-ray in Fig. 4), but resembles in most characters the described holotype (see Fig. 4). Length of left forelimb 29.2 mm; length of left hind limb 36.4 mm (for additional measurements see Table 2). Nasal also tubular, but directed more laterally and only slightly dorsally. Nasal scale on the canthus rostralis, and partly visible from above. Between ear opening and eye, a round slightly swollen patch consisting of several scales is present. Gular fold and a small gular pouch present. Neck crest more strongly developed than in holotype, also consists of nine scales, but longer. Single conical scales framing the ear opening longer, tufts of spinose scales behind the ear and on the side consist of more scales. Occipital scale large, but bordered by a broad elongated scale on each side. Dorsal scales partly mucronate. Tail short and thin, only about one third longer than the snout–vent length; base of the tail not notably broadened. Entire dorsal surface of body, tail, and limbs brownish with obscure irregularly placed lighter and darker shades. Belly and underside of the tail dirty whitish. Throat dirty whitish, becoming finely marbled posteriorly, uniform dark patch at its base present. *Subadults.* Both resemble the holotype but characters are not as distinct. Nasal scale slightly above the canthus rostralis, visible from above. In MCZ R-146688, the same swollen patch as in the female is recognizable. Neck crests present in both specimens but weakly developed, consisting of 10 and 11 erect scales. Coloration as in other juvenile *Agama* lizards; four dark crossbars between the limbs, becoming broad at the vertebral area, showing a pale, darkly framed, diamond-shaped patch at each crossband. In MCZ R-146685, a pale vertebral stripe is visible. Throat coloration resembles the holotype, extending to the anterior part of the belly. *Juvenile.* MCZ R-146686 resembles the holotype, but characters are only rudimentarily developed. Occipital scale large, covering about two thirds of the back parts of the head. Coloration similar to the described subadults.

Etymology. The entire Omo River basin is an important area both geologically and archaeologically and several hominid fossils have been excavated there. Reflecting the authors' interest in the evolution of early humans, this new species is named after "Lucy," the famous hominid fossil of *Australopithecus afarensis* Johanson, White, and Coppens, 1978, found in the Hadar area (the northern offshoot of the Rift System) of Ethiopia.

Ecology. Based on catalogue data, the entire MCZ type series was collected on the same day. The series contains two adults, two subadults and one juvenile specimen. Gartshore (1985) mentioned both *A. weidholzi* and *A. gracilimembris* as annual species because she found gravid females between April and May, but rarely observed adults after June and none after the end of August; the first juveniles were found thereafter. So, adult and juvenile specimens were never collected at the same time. In *Agama lucyae* sp. nov., a gravid female was collected in July (gravid females of *A. persimilis* have been

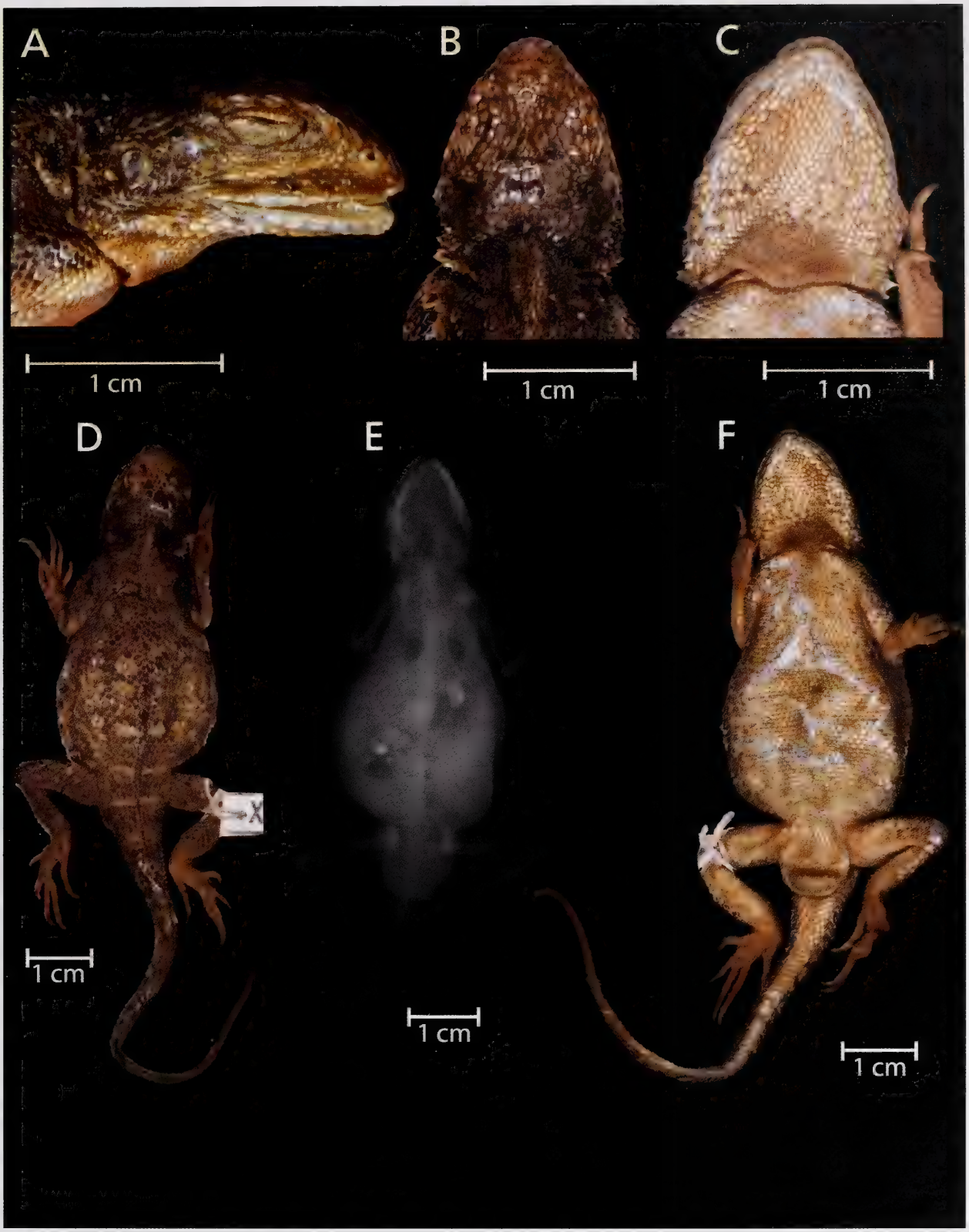

Figure 4. Adult female paratype of *Agama lucyae* sp. nov. (MCZ R-146687). A, Lateral view of head; B, dorsal view of head; C, ventral view of head; D, dorsal view; E, X-ray, ventral view; F, ventral view.

TABLE 1. COMPARISON OF SMALL TO MEDIUM-SIZED *AGAMA* SPECIES.

	A. weidholzi	*A. gracilimembris**	*A. rueppelli*	*A.persimilis#*	*A. hartmanni*	*A. lucyae sp. nov.*
SVL female (mm)	56.0–65.0	49.0–57.0	76.0–88.0	56.0–64.0	—	58.5
SVL male (mm)	54.0–62.0	44.0–47.0	58.0–88.0	43.0–54.0	87.0–92.0	53.5
Dorsal body scalation	Homogeneous	Heterogeneous	Homogeneous	Homogeneous	Homogeneous	Homogeneous
Position of nasal scale relative to canthus rostralis	Below	Below	On	Above	On	On
Dorsal scales	Keeled, not mucronate	Keeled, not mucronate	Keeled, mucronate	Keeled, mucronate	Keeled, not mucronate	Keeled, not mucronate
Gular scales	Keeled	Keeled	Smooth	Smooth	Smooth	Smooth
Ventral scales	Keeled	Keeled	Smooth	Smooth	Smooth	Smooth
Midbody scales	68–82	70–85 ($\bar{X}$ 74.8)	54–64	52–57	76–81	66–69 ($\bar{X}$ 67.4)
Vertebral scales	32–48 ($\bar{x}$ 38.0)	30–46 ($\bar{X}$ 37.0)	59–66	26–31	61–68	47–52 ($\bar{X}$ 50.4)
Nuchal crest	Absent	Absent	Absent	Absent	Absent	Present
Dorsal head scales	Smooth	Strongly keeled	Smooth, feebly keeled	Smooth, feebly keeled	Smooth, feebly keeled	Smooth, feebly keeled
Fourth-toe lamellae	16–21	13–14	14–16	16–18	16–21	17–18
Tufts of spines behind ear and on side of the neck	Absent	Absent	Present	Present	Absent	Present

*=partly according to Grandison (1968); #=party according to Parker (1942).

TABLE 2. MEASUREMENTS AND PHOLIDOSIS OF THE TYPE SERIES OF *A. LUCYAE* SP. NOV.[a]

	MCZ R-146689 *Holotype*	MCZ R-146687 *Paratype*	MCZ R-146686 *Paratype*	MCZ R-146685 *Paratype*	MCZ R-146688 *Paratype*
SVL	53.5	58.6	25.0	39.9	39.5
TL	–	77.3	31.9	62.9	63.0
HW	12.2	12.2	6.1	9.5	9.2
HL	16.6	16.3	8.9	12.1	12.3
HH	7.5	7.1	4.5	6.5	5.9
SL	10, 8	8, 8	9, 10	10, 9	9, 9
IL	9, 8	9, 9	8, 8	10, 9	9, 9
SaM	67	68	69	67	66
VS	68	68	62	65	64
DS	52	50	47	52	51
PP	8	—	9	9	—

[a]See Material and Methods for abbreviations. For SL and IL the first numbers refer to the left and the second to the right side of the specimen.

found in August; see Spawls et al., 2002), together with a relatively freshly hatched juvenile (MCZ R-146686) and two subadults (MCZ R-146685, 146688). Thus, *A. lucyae* sp. nov. should not be an annual lizard like the other two dwarf species (*A. weidholzi, A. gracilimembris*), as three different age phases were collected on the same day.

Distribution. There is some confusion about the exact location of the type locality. The original collection label shows only "Wollega" [=Welega or Wellega] as the province, whereas the MCZ online register gives both Wollega and Shewa. However, the border of Wollega is approximately 200 km distant from the type locality (58 km NW of Soddo). If the correct locality is actually in the Omo Gorge, then it would lie within either Kefa [=Kaffa] Province (west bank) or Shewa [=Shoa or Showa] Province (east bank). These provincial divisions have, since 1996, been replaced by ethnically based administrative regions (*kililoch*) with different boundaries. Today the west bank of the Omo Gorge lies within Oromiya [=Oromia, also called "Region 4"], whereas the east bank is in the Southern Nation, Nationalities, and Peoples' Region [also called "Southern Peoples' Region"]. The coordinates given are not part of the original label and have an error of 29.205 km according to the MCZ database.

Agama lucyae sp. nov. is currently only known from its type locality, which lies to the west of the Rift Valley. Two distributional scenarios are possible. (a) A distribution further west to Sudan and northwestern Kenya, more likely than to Somalia, and (b) a restricted distribution in the Central Ethiopian highlands. However, *A. lucyae* sp. nov. is the only dwarf species collected within the Ethiopian highlands (Fig. 2) and presumably is a rock- or rocky-ground–living species rather than a dweller on sandy surfaces. The Ethiopian Plateau is a volcanic system of 3,000-m-deep basalt rocks on underlying marine rocks, whereas the surrounding arid areas are sandy grassland, savannas, and deserts (Largen and Spawls, 2010). Therefore, (b) is perhaps the more likely distribution scenario, although numerous lowland species are known to move upstream in the deeply dissected gorges, sometimes even extending onto the plateau lands (Stephen Spawls personal communication).

The types of *Agama lucyae* sp. nov. were collected near the Omo River. This river

arises in an alpine environment and passes through rainforest, open savannah and finally through desert and is the sole Ethiopian feeder of Lake Turkana (the Kerio and Turkwell rivers feed the lake within Kenya). The locality is in the central part of the river system, which based on the examination of satellite images, is primarily rocky, semi-arid, open bushland lacking dense vegetation. However, the terrain in this area changes dramatically. The northwest side of the Omo Gorge drops down from more than 3,000 m altitude to less than 1,000 m in only about 16 km, and the gorge itself has steep cliffs. Therefore, the specimens could have been collected in highland or lowland and in any of several different vegetation types because parts of the gorge are quite densely vegetated, although there are also extensive sand flats.

DISCUSSION

Small species are not rare in *Agama* (e.g., there is a species radiation with about seven species in southern Africa), but most often small size is associated with solitary living, rather than with harem groups as seen in the large rock agamas (Branch, 1998; Spawls et al., 2002). However, solitary agamas are often found in lower densities and the collection of a series of all age classes could indicate a group living structure.

A new agamid species from the Horn of Africa is not surprising. The area is both one of the African hotspots for arid-adapted reptiles and one of the most poorly studied areas of the continent (Largen and Spawls, 2010). This is certainly true of agamid lizards. In most species, many aspects of ecology, habitat preferences, and behavior are unknown, and several (e.g., *A. hartmanni*, *A. persimilis*) are only known from a handful of voucher specimens from two or three localities. However, on the basis of known distributions (see Fig. 4), these species prefer lowland and sandy savannas or semideserts, whereas *A. lucyae* sp. nov. was found in the Central Ethiopian highlands. The highlands of the Rift Valley in Ethiopia seem to be a distribution barrier for ground-living agamas within the Horn. *Agama persimilis* is distributed in eastern Ethiopia and Somalia (like *A. robecchii*, not shown), southward to Kenya, whereas *A. hartmanni* is known from lowlands of the western side of the Rift in Sudan, South Sudan, and Eritrea. Only *A. rueppelli* occurs on both sides. The Ethiopian Rift Valley and its southern offshoots could also be the contact zone between two important species radiations, the West African *Agama agama* group and the East African *A. lionotus* group, as represented, for example, by *A. finchi,* a member of the former, and *A. lionotus,* a member of the latter group, neither of which crosses the Valley (Böhme et al., 2005), but *A. doriae* (not closely related to either group) is known from the Omo Gorge near the *A. lucyae* sp. nov. collection locality (Stephen Spawls, personal communication). On the other hand, species of the agamid genus *Acanthocercus* occur on both sides of the Rift but are distinct in habitat preferences to *Agama*. In contrast, *A. lucyae* sp. nov. was found in the center of an area not previously known to support ground-living *Agama* lizards.

The relationships of *A. lucyae* sp. nov. remain unclear. On the basis of morphology and zoogeography, it could be closely related to *A. hartmanni*, but a relationship to *A. gracilimembris, A. persimilis,* or *A. rueppelli* is also feasible. On the basis of zoogeography, a membership in the *A. agama* or *A. spinosa* (including *A. hartmanni*, unpublished data) radiations is more likely than in the *A. lionotus* radiation, given its occurrence west of the Rift Valley (Wagner et al., 2011). However, the relations of these species are also currently poorly resolved.

ACKNOWLEDGMENTS

We are grateful to José Rosado and Jonathan Losos for access to the MCZ collection and for the loan of the specimens and to Wolfgang Böhme (ZFMK), Michael Barej and Frank Tillack (ZMB), Ivan Ineich (MNHN), Andreas Schmitz (MHNG), and Heinz Grillitsch (NHMW) for contribution of images or access to their respective collections. The manuscript was improved by insightful comments from Stephen Spawls and Wolfgang Böhme. We are grateful to the Museum of Comparative Zoology, Harvard University, for permission to publish photographs of their specimens. All original photography of MCZ specimens is copyright ©President and Fellows of Harvard College. This research was supported in part by the Lemole Endowed Chair in Integrative Biology Fund at Villanova University.

Appendix 1. Material Examined

Agama bottegi. *Somalia.* Lugh (MSNG 28548, holotype); Karin, 10°58′26.4″ N, 49°12′49.2″ E (CAS 227496).

Agama gracilimembris. *Benin.* Without locality (MNHN 04.114-5; syntypes). *Cameroon.* Benue NP (ZFMK 33717); Boki (ZFMK 15257–259) *Central African Republic.* Koumbala (ZFMK 33718–721); between Kotissako and Sakoumba (ZFMK 33722–725).

Agama hartmanni. *South Sudan.* Bahr el Ghazal, Meschrael Rek (ZFMK 2587); Bahr el Zeraf (ZFMK 2586); Boma Hills (ZFMK 27598); 20 mi N Faschoda [=Kodok] (BMNH 1901.7.31.1); Rejaf (MCZ R-29639). *Sudan.* Dongola (ZMB 4355 [3 ex., type series]); Singa (BMNH 1913.9.16.9).

Agama lucyae **sp. nov.** *Ethiopia.* Shewa Province, Wollega, Omo River, 58 km NW of Soddo, about 1,300 m a.s.l., 7.27085°N, 37.37891°E (MCZ R146685–89).

Agama persimilis. *Ethiopia.* Haud (45°50′E, 8° N, BMNH 1937.12.5.64 [new: 1946.8.24.51], holotype). *Kenya.* East of Wajir at Wajir Bor (MHNG 2236.20).

Agama rueppelli. *Kenya.* Kanapoi (MCZ R-128427); Kerio River Camp (MCZ R-140858); Lake Turkana 2°18′N; 36°03′E (ZFMK 30694–695); Lodwar (MCZ R-39013, 84292); Lokori (MCZ R-84286); Loperot Kalabata (MCZ R-97175); Marsabit, 60 mi N (MCZ R-84290); Mbunyi near Taveta (MCZ R-18280); Voi (MCZ R-41003, 41005, 41008); Voi (MCZ R-18281, syntype *A. r. septentrionalis*); South Turkana (MCZ R-97168–71). *Somalia.* Buran district (MCZ R-49120). *South Sudan.* Bahr-el-Gebel, Redjaf [=Rejaf] (ZFMK 2588–89); (?) Bender-Meraya (BMNH 1946.8.28.5, syntype of *A. r. rueppelli*).

Agama weidholzi. *Mali.* Between Negala and Kassaro (ZFMK 20059); Fatao, 9 km N (ZFMK 20063–065); Kassaro, 8 km E (ZFMK 20060); Kita, 5 km E (ZFMK 20061); Kita, 20 km E (ZFMK 20062). *Senegal.* Between Tiara und Mantiankani (ZFMK 20072); Casamance: 13 km SW Kolda (ZFMK 20073–078); Darsalam, 5 km SE (ZFMK 20066–068); Kounkané, 12 km W (ZFMK 20070–071); Medina Gounas, 20 km S (ZFMK 20069); Tabadienka, 30 km S Diallakoto (NHMW 18318; 18319:1–2, 4–8; MCZ R-44311–312 type series).

Appendix 2. Material Cited for Distributional Information Only

Agama gracilimembris. *Central African Republic.* Ndellé (MNHN 17.191). *Nigeria.* Igbetti (ZMC R36654, R36701, R36263); Kano (BMNH 1961.2067–8, 1962.566); Lafia (BMNH 1938.3.1.47); Shendam (BMNH 1962.1570); Wukari (BMNH 1938.3.1.48-9); Zaria (NHMW 18994); Zonkwa (BMNH 1961.949, 1962.1569).

Agama hartmanni. *Eritrea.* ("Um Ager [=Omhajer], Missione Corni, Calciati," type locality of *A. cornii*). *South Sudan.* Taufikia (NHMW 17039).

Agama persimilis. *Ethiopia.* Bohodle (BMNH 1937.12.5.68–73, 1946.8.27.55–60). *Kenya.* Kitui Dist.: 7.7 km S of Ngomeni, Tolotwa (CAS 161295); Mandera Dist: ca. 1 mi. NE. Mandera Dist.: Elev. 1,200 ft. (CAS 130307). *Somalia.* Bud Bud (MF 5331–32); Dùsa Marèb, 55 km N-NE of (MF 5459); El Bur [=Ceel Buur] (MF 2431); Geribàn (MF 3865-66); Har Addèi (MF 5456); Iesòmma (MF 5189).

Agama rueppelli. *Ethiopia.* Dabanac (MSNG 28905); Gumboworen (ZMB 27387); Sassabana (BMNH 95.12.31.2). *Kenya.* Kajiado, 20.8 km N of (CAS 198918); Kakuma (CAS 130877); Lake Baringo, Kampi-Ya-Samaki (CAS 131599); Lokichoggio (CAS 131247); Lokitaung (CAS 131281); Loyengalani (CAS 123106). *Somalia.* Boorama, Awdal Region (MVZ 241339); Buq Village, 27 km NE by Baargaal Rd. (MVZ 242741); Hargeysa Airport, 6 km E by Bander Wanaaq Rd. (CAS 225501). *South Sudan.* Lokomarinyang (CAS 131530).

Appendix 3. Localities Obtained from Literature Used for Distributional Information

Agama gracilimembris. *Benin.* Pendjari NP (Ullenbruch et al., 2010). *Central African Republic.* Ndellé, 8°25′N, 36′E (Grandison 1968). *Ghana.* Wa (Spawls *in* Gartshore, 1985). *Nigeria.* Ado-Awaiye, Anara, Falgore, Hung, Kura, Pandam, Ringum, Yankari (all Gartshore, 1985).

Agama rueppelli. *Ethiopia.* Confluence of the Web and Ganana [Ganale] (Largen and Spawls, 2006).

REFERENCES

Bauer, A. M., T. R. Jackman, E. Greenbaum, V. Giri, and A. De Silva. 2010. South Asia supports a major endemic radiation of *Hemidactylus* geckos. *Molecular Phylogenetics and Evolution* **57:** 343–352.

Böhme, W. 1975. Zur Herpetofaunistik Kameruns, mit Beschreibung eines neuen Scinciden. *Bonner zoologische Beiträge* **26:** 2–48.

———, P. Wagner, P. Malonza, J. Köhler, and S. Lötters. 2005. A new species of the *Agama agama* group (Squamata: Agamidae) from western Kenya, East Africa, with comments on *Agama lionotus* Boulenger, 1896. *Russian Journal of Herpetology* **12:** 143–150.

Boulenger, G. A. 1895. Rettili e Batraci, pp. 9–18. *In* G. Doria, and R. Gestro eds. *Esplorazione del Giuba e dei suoi Affluenti compiuta dal Cap. V. Bottego durante gli Anni 1892-93 sotto gli auspicii della Società Geografica Italiana.* Annali del Museo Civico di Storia Naturale Giacomo Doria, vol. 2, no. 15. Genoa, Museo civico di storia naturale.

———. 1898 [1897]. Concluding report on the late Capt. Bottego's collection of reptiles and batrachians from Somaliland and British East Africa. *Annali del Museo Civico di Storia Naturale di Genova* **2**(18): 715–723.

Branch, W. R. 1998. *Field Guide to Snakes and Other Reptiles of southern Africa*, 3rd ed. Sanibel Island, Florida, Ralph Curtis Books.

Brygoo, E. R. 1988. Les types d'agamides (reptiles, sauriens) du Museum national d'Histoire naturelle. Catalogue critique. *Bulletin de la Muséum nationale d'Histoire naturelle Paris,* Section A. Zoologie, Biologie et Ecologie *Animales* **10**(3)(Suppl.1): 1–56.

Chabanaud, P. 1918. Étude complémentaire de deux *Agama* de l'Afrique occidentale et description de quatre espèces nouvelles de reptiles de la même région. *Bulletin de la Muséum nationale d'Histoire naturelle Paris* **24:** 104–112.

Gartshore, M. E. 1985. *Agama gracilimembris* in Nigeria. *The Herpetological Journal* **1:** 23–25.

Grandison, A. G. C. 1968. Nigerian lizards of the genus *Agama* (Sauria: Agamidae). *Bulletin of the British Museum of Natural History (Zoology)* **17:** 65–90.

———. 1969. *Agama weidholzi* of West Africa and its relationship to *A. gracilimembis. Bulletin de l'Institute Fondamental d'Afrique Noire (Ser. A)* **31:** 666–675.

Guibé, J. 1954. *Catalogue des Types de Lézards du Muséum national d'Histoire naturelle.* Bayeux, France, Colas.

Joger, U. 1990 [1991]. The herpetofauna of the Central African Republic, with description of a new species of *Rhinotyphlops* (Serpentes: Typhlopidae), pp. 85–102. *In* G. Peters, and R. Hutterer eds. *Vertebrates in the Tropics.* Bonn, Museum A. Koenig.

Lanza, B. 1978. On some new or interesting East African amphibians and reptiles. *Monitore Zoologico Italiano N.S. , Supplemento* **10:** 229–297.

———. 1983. A list of the Somali amphibians and reptiles. *Monitore Zoologico Italiano N.S., Supplemento* **18:** 193–247.

LARGEN, M., AND S. SPAWLS. 2006. Lizards of Ethiopia (Reptilia Sauria): an annotated checklist, bibliography, gazetteer and identification key. *Tropical Zoology* **19:** 21–109.

———, AND ———. 2010. *The Amphibians and Reptiles of Ethiopia and Eritrea.* Frankfurt am Main, Chimaira Publishing.

MOODY, S. M. 1980. Phylogenetic relationships and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). Unpublished PhD Thesis. Ann Arbor, University of Michigan.

PARKER, H. W. 1942. The lizards of British Somaliland. *Bulletin of the Museum of Comparative Zoology* **91:** 1–101.

PETERS, W. C. H. 1869. Eine Mittheilung über neue Gattungen und Arten von Eidechsen. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften Berlin* **1869:** 57–66.

SCORTECCI, G. 1929. Rettili dell'Eritrea esistenti nelle Collezioni del Museo Civico de Milano. *Atti della Società Italiana di Scienze Naturali, e del Museo Civico di Storia Naturale Milano* **67**(3–4): 290–339.

SPAWLS, S., K. M. HOWELL, R. DREWES, AND J. ASHE. 2002. *A Field Guide to the Reptiles of East Africa.* London and San Diego, Academic Press.

ULLENBRUCH, K., O. GRELL, AND W. BÖHME. 2010. Reptiles from southern Benin, West Africa, with the description of a new *Hemidactylus* (Gekkonidae), and a country-wide checklist. *Bonn Zoological Bulletin* **57:** 31–54.

VAILLANT, M. L. 1882. Reptiles et Batraciens, pp. 1–10. *In* G. Révoil ed. *Mission dans le pays Comalis, Faune et Flore. Faune et Flore des Pays Comalis, Afrique Oriental.* Paris, Challamel Ainé Éditeur.

WAGNER, P. 2010. Diversity and distribution of African lizards. Unpublished Ph.D. Thesis. Bonn, Germany, University of Bonn.

———. 2011. Book review: the amphibians and reptiles of Ethiopia and Eritrea. *Salamandra* **47:** 61–62.

———, W. FREUND, D. MODRÝ, A. SCHMITZ, AND W. BÖHME. 2011. Studies on African *Agama* IX. New insights into *Agama finchi* Böhme et al., 2005 (Sauria: Agamidae), with the description of a new subspecies. *Bonn zoological Bulletin* **58:** 25–34.

———, I. INEICH, A. LEACHÉ, T. M. WILMS, S. TRAPE, W. BÖHME, AND A. SCHMITZ. 2009. Studies on African *Agama* VI. Taxonomic status of the West African *Agama* (Sauria: Agamidae) with prominent tail crests: *Agama boulengeri* Lataste 1886, *Agama insularis* Chabanaud, 1918 and *Agama cristata* Mocquard, 1905. *Bonner zoologische Beiträge* **56:** 239–253.

WERMUTH, H. 1967. Liste der rezenten Amphibien und Reptilien: Agamidae. *Das Tierreich* **86:** 1–127.

WETTSTEIN, O. 1932. Eine neue Eidechse aus Senegambien. *Zoologischer Anzeiger* **99:** 303–305.